

# Exploring the tug of war between positive and negative interactions among savanna trees: Competition, dispersal, and protection from fire.

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## Abstract

Savannas are characterized by a discontinuous tree layer superimposed on a continuous layer of grass. Identifying the mechanisms that facilitate this tree-grass coexistence has remained a persistent challenge in ecology and is known as the “savanna problem”. In this work, we propose a model that combines a previous savanna model (Calabrese et al., 2010), which includes competitive interactions among trees and dispersal, with the Drossel-Schwabl forest fire model, therefore representing fire in a spatially explicit manner. The model is used to explore how the pattern of fire-spread, coupled with an explicit, fire-vulnerable tree life stage, affects tree density and spatial pattern. Tree density depends strongly on both fire frequency and tree-tree competition although the fire frequency, which induces indirect interactions between trees

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and between trees and grass, appears to be the crucial factor controlling the tree-extinction transition in which the savanna becomes grassland. Depending on parameters, adult trees may arrange in different regular or clumped patterns, the later of two different types (compact or open). Cluster-size distributions have fat tails but clean power-law behavior is only attained in specific cases.

*Keywords:* Savanna, tree-tree competition, tree-grass equilibrium, individual based model, clustering, fire-spread model

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## 1. Introduction

Savanna ecosystems are characterized by the robust coexistence of trees and grass. The mechanisms allowing for the persistence of both types of vegetation and governing the population dynamics and spatial arrangement of savanna trees are poorly understood (Scholes and Archer, 1997; Bond, 2008). Of the many potential driving mechanisms investigated, local-scale interactions among trees have received increasing attention in recent years (Barot et al., 1999; Wiegand et al., 2006; Meyer et al., 2008, 2007a,b; Scanlon et al., 2007; Calabrese et al., 2010). Such tree-tree interactions can roughly be divided into two classes: facilitative and competitive. Facilitation among trees promotes tree clustering and may be mediated by a variety of mechanisms such as limited-range dispersal, improvement of local resource conditions, and protection from fire (Belsky et al., 1989; Hochberg et al., 1994; Holdo, 2005; Scanlon et al., 2007; Calabrese et al., 2010).

Alternatively, competition among trees for water, nutrients, and light may constrain tree density and favor tree-grass coexistence, as well as promot-

ing spatial separation between trees (Barot et al., 1999; Meyer et al., 2008; Calabrese et al., 2010).

There is evidence for both classes of interactions in the savanna literature, sometimes coming from the same region. For example, several studies have found evidence consistent with competition in the Kalahari (Skarpe, 1991; Jeltsch et al., 1999; Moustakas et al., 2006, 2008; Meyer et al., 2008), while others have found evidence suggesting facilitation (Caylor et al., 2003; Scanlon et al., 2007). Indeed, one of the key difficulties in understanding the forces structuring savanna tree populations is that both classes of local-scale interactions often occur together and it is not obvious whether the net effect of local interactions on tree population dynamics will be positive or negative (Bond, 2008). Further studies, both empirical and theoretical, are needed to better understand the interplay between these opposing forces. Specifically, studies that focus on a limited number of processes and their interactions should help illuminate the conditions under which positive or negative local interactions structure savanna tree populations.

Mesic savannas that receive 400-800 mm of mean annual precipitation (MAP) are particularly interesting because there is evidence from such systems that, in addition to local-scale interactions, fire plays an important role. (Sankaran et al., 2005; Bucini and Hanan, 2007). Both of these factors can act strongly on juvenile trees and can contribute to a demographic bottleneck through which juvenile trees must pass to recruit into the adult population. In contrast to forest tree species, savanna trees are often more fire resistant (Hoffmann et al., 2003), thus savanna fires effectively burn the grass layer and the young trees included in it, leaving adult trees alive, af-

fecting only tree recruitment and not adult survival (Gignoux et al., 1997). Recent studies highlighting the importance of tree competition and/or fire on savannas are Higgins et al. (2000), Moustakas et al. (2006), Moustakas et al. (2008), D’Odorico et al. (2006), Hanan et al. (2008), Meyer et al. (2008), or Calabrese et al. (2010). From their results we might expect a kind of tug of war between these forces, the outcome of which affects both the tree-grass balance of the savanna and the spatial arrangement of adult trees.

The role of fire in mesic savannas is two-fold. On the one hand, it provides an indirect way for grass to compete against trees: the higher recovery rates of grasses compared to juvenile trees make grass the dominant form of vegetation shortly after a fire has destroyed both. On the other hand, several studies have suggested that adult trees can protect vulnerable juveniles from fire, thus increasing their chances of survival (Hochberg et al., 1994; Holdo, 2005), but this protection effect has not been intensively studied. However, given the frequent occurrence of fires in many savannas, it seems likely that the protection effect may be one of the most common facilitative interactions among savanna trees, and the dominance of grass after fire could be as important as tree-tree competition in restricting the amount of tree-cover in the savanna.

Recently, Calabrese et al. (2010) studied the interaction between competition and fire in a highly simplified savanna model. They showed that these two forces interact non-linearly with sometimes surprising consequences for tree population density and spatial pattern. However, because Calabrese et al. (2010) treated fire in a non-spatially explicit manner, only the negative impact on trees, and not the protection effect, was included and thus they

could not fully tease apart how these contrasting local interactions function in combination.

Here, we focus on a spatially explicit lattice model of savanna tree and grass population dynamics under the influence of competition and fire. The model is an extension of the semi-spatial model studied by Calabrese et al. (2010). Importantly, both competition and fire are spatially explicit processes in the new model. This allows us to study directly how adult trees influence the survival probabilities of nearby juveniles. We treat competition in the same way as in Calabrese et al. (2010) and fire is implemented in a similar manner as in the Drossel-Schwabl forest fire model from statistical physics (Drossel and Schwabl, 1992). In contrast to adult trees in the Drossel-Schwabl model, grasses and juvenile trees are the flammable objects in our case. We highlight the ranges of conditions under which local interactions result in net positive and net negative influences on juvenile tree recruitment, and we demonstrate how these local interactions affect the density and spatial structure of adult-tree populations.

## **2. Spatially explicit fire models**

Bak and Chen (1990) introduced a simple forest fire model to demonstrate the emergence of scaling and fractal energy dissipation. Drossel and Schwabl (1992) extended this model by introducing a lightning or sparking parameter  $f$ , and this is the forest fire model we have adapted to study fire spread in savannas. It is one of the best studied examples of non-conservative, self-organized criticality (Bak and Chen, 1990; Grassberger and Kantz, 1991; Drossel and Schwabl, 1992; Clar et al., 1996, 1999; Schenk et al., 2000). The

forest fire model is a probabilistic cellular automaton defined on a 2-dimensional lattice of  $L^2$  sites, initialized with a combination of burning trees and live trees, and updated at each time-step with the following four simple rules: (i) A burning tree becomes an empty site. (ii) A live tree becomes a burning tree if at least one of its nearest neighbors is burning. Some immunity can be introduced in this rule, so that a green tree becomes a burning tree with probability  $1 - I$  (Clar et al., 1996). (iii) A new tree establishes at an empty site with probability  $r$ . (iv) Live trees in the lattice spontaneously (i.e., without the need of a burning neighbor) ignite with probability  $f$ . This model displays very rich behavior, and depending on the parameters  $f$  and  $r$ , it features spiral-like fronts, critical states and phase transitions. Furthermore, while the Drosel-Schwabl model is minimalistic, it produces burn patterns similar to those observed empirically, and is closely related to more detailed wildfire models (Zinck and Grimm, 2009).

### 3. Savanna Fire Model (SFM)

Our model is run in a square lattice with periodic boundary conditions. We use a lateral size of  $L = 200$  sites, so that there are  $N = L \times L = 4 \times 10^4$  lattice sites in the simulation domain. Each site represents a savanna square of 5 meters on a side. In the previous savanna model (SM) of Calabrese et al. (2010), each site in the lattice could be in one of two states: grass- or tree-occupied. The savanna fire model (SFM) introduced here combines the previous SM and the above-described Drossel-Schwabl Forest Fire model, but with the flammable components being grass and juvenile trees. In this way, fire is included explicitly as a possible state in the dynamics. The SFM con-

siders three new states in addition to the two in the SM so that each site on the lattice can be in one of the following five states: Grass (G), Juvenile Tree (JT), Adult Tree (AT), Burning (B) and Ashes (A).

We can distinguish two interaction neighborhoods for each lattice site: the *near* neighborhood consists of the eight sites sharing an edge or a corner with the central one (Moore neighborhood), and we assume this is the spatial scale at which direct competition among trees occurs. The *far* neighborhood consists of the sixteen additional sites surrounding the *near* ones and sharing edges or corners with them. They will be assumed to be the farthest sites to which seeds from a focal tree can arrive.

We note that fire propagation occurs over a much shorter timescale (the spread rate may be around 2 m/s, see Cheney and Gould (1995)) than tree growth, reproduction, death, and other ecological processes. Thus we implement the burning process on top of the previous SM, but acting on a faster scale. Specifically, at each time step, time advances by  $\Delta t = 0.1$  years, and the whole lattice is scanned in parallel to check for one of the following updates:

1. Growth: A random number is drawn for each site occupied by a juvenile tree so that with probability  $m\Delta t$  it becomes an adult tree. Thus  $m^{-1}$  is the mean time for a juvenile tree to become adult.
2. Reproduction and establishment: Each adult tree in the lattice sends, with probability  $b\Delta t/24$ , a seed to each of the 24 sites within its *near* and *far* neighborhood. If the seed lands on a site in a state which is neither G nor A, then nothing happens (establishment fails). If instead a site occupied by grass or ashes is reached a juvenile tree is established.

3. Competition: A juvenile tree survives competition with neighboring adult trees with probability  $P_C^{Surv}$ . This survival probability depends only on the competition exerted by neighboring adult trees:  $P_C^{Surv} = e^{-\delta S_1}$ , where  $\delta$  is the competition parameter and  $S_1$  is the number of adult trees in the *near* neighborhood.
4. Death: A random number is drawn for each site occupied by an adult tree, so that with probability  $\alpha\Delta t$  this tree dies. Thus  $\alpha^{-1}$  is the average adult-tree lifespan.
5. Recovery: At each time step, each ash site may recover into grass with probability  $r\Delta t$ , so that  $r^{-1}$  is the mean recovery time of grass from ashes. Note that this forces a delay between successive fire fronts, thus preventing the lattice from continually burning.
6. Spontaneous burning: There is a “lightning parameter”,  $f$ , so that fire appears spontaneously on the lattice at this rate, affecting grass and juvenile trees. More explicitly, lattice sites occupied by G and JT are checked so that with probability  $f\Delta t/N$  they become burning sites.
7. Fire propagation and extinction: After updating with all the above processes, a new pass through the lattice is done, so that if some fire has been introduced in the previous step, fire propagation is simulated until the fire burns out. As previously mentioned, we assume that this process is fast and occurs on a much shorter timescale than the  $\Delta t = 0.1$  years introduced above. It is implemented in the following way:
  - a) Each G and JT site is checked and if at least one site in its *near* neighborhood is in the B state, the site also burns with probability



$1 - I$ , where  $I \in [0, 1]$  is an *immunity* parameter. This models fire propagation on grass and juvenile trees. Note that, since adult trees do not burn, fire has a lower chance of reaching JT (and G) sites which are surrounded by some adult trees. The inclusion of fire in a spatially explicit manner therefore implements the protection effect from adult trees.

- b) End of burning: All sites that were burning before entering the previous step (a) are set to ashes.

Processes a) and b) are repeated until no burning sites remain. Time then advances  $\Delta t$  units and the algorithm repeats again from step (1) on the updated lattice.

Table 1: Parameters

Parameters		Units
$\alpha$	adult-tree mortality rate	$0.01 \text{ year}^{-1}$
$b$	seed dispersal rate	$0.05 \text{ year}^{-1}$
$\delta$	tree competition coefficient	vary
$f$	lightning parameter	$0.33 \text{ year}^{-1}$
$m$	juvenile tree maturation rate	$0.1 \text{ year}^{-1}$
$r$	grass recovery rate	$4 \text{ year}^{-1}$
$I$	fire immunity	0.3

The core parameters used (see Table 1) are based on those of Calabrese et al. (2010), but with a few modifications. The adult-tree death rate,  $\alpha$ , and the lightning parameter,  $f$ , were changed according to Hanan et al. (2008, pag.

852) and Gignoux et al. (1997, pag. 557), respectively. In mesic savannas fire frequency is about once per year to once every three years (Hanan et al. (2008, pag. 852) and Gignoux et al. (1997, pag. 557)) so we set  $f = 0.33$ . The juvenile tree growth rate,  $m$ , was determined from Hochberg et al. (1994, pg. 219), so that in the absence of fire, a juvenile tree takes on average 5 years to reach the adult state. These parameters will be used through the paper unless explicitly stated.

The spatially-limited dispersal of seeds from an adult to neighboring sites, one of two key facilitative processes in the model, occurs at the spatial scale of the first and second neighborhood, whereas the main negative interaction, adults competing with and inhibiting the development of juvenile trees, occurs only at the scale of the first (near) neighborhood.

This is the opposite situation as the one believed to occur in extremely arid ecosystems, namely short distance facilitation by local improvement of water infiltration, and long range competition among plants mediated by long superficial roots. In this last case, vegetation patterns are expected to display a rather regular tree or patch spacing (Rietkerk et al., 2004; Rietkerk and van de Koppel, 2008). Our situation is more appropriate for mesic savannas, and would tend to promote tree clustering. But the occurrence of fire may alter the nature of the interactions in a variety of ways, which we investigate in the following.

#### **4. The tree-grass balance and tree extinction**

As expected, stronger tree-tree competition shifts the tree-grass balance in favor of grasses (Figure 1, left). The model was run for 5000 years to ensure

an asymptotic state was reached in which we performed the measurements described in Figure 1. Simulations were performed to determine under which conditions a transition from savannas to grassland occurs.

Similarly to the results Calabrese et al. (2010) obtained for their fire parameter  $\sigma$ , the lightning frequency  $f$  turns out to be the parameter with the strongest influence on the savanna-grassland transition in the SFM: The right part of Figure 1 shows a phase transition from savanna to grassland driven by increasing  $f$  (*c.f.* Figure 2 in Calabrese et al. (2010)).

Frequent fires prevent juvenile trees from recruiting into the adult population, and if this inhibition is strong enough, it would eventually result in tree extinction. This mechanism and the subsequent tree extinction it causes was implicitly contained in the definition of the fire parameter in the SF of Calabrese et al. (2010). Here, the mechanism appears as a consequence of the explicit presence of fire.

## **5. Positive and negative effects of surrounding adult trees on juvenile's: Protection vs. competition**

In addition to affecting the tree-grass ratio, fire also introduces the positive effect of juvenile tree protection by surrounding adult trees. To analyze this effect in detail we ran simulations in which only the fire propagation process (step 7 in the above algorithm) occurs. The lattice is initialized fully with grass except for one unique site occupied by a juvenile tree, and a number of adult trees, from 1 to 8, occupying random positions in the Moore neighborhood of the JT. Given this initial condition, one sparking is allowed so that a lattice site chosen randomly among the G sites burns and fire begins

to propagate. Step 7 in the SFM algorithm is repeated until fire disappears.

Juvenile trees sufficiently protected by adult trees will not burn. An example is seen in Fig. 2, where the pass of a fire front does not affect a juvenile protected by five adult trees.

We quantified this effect by repeating the burning protocol 1000 times for each number of AT neighbors, from 1 to 8. The sparking site and the position of the surrounding neighbors is changed randomly in each of these realizations. The resulting survival probability  $P_F^{Surv}(S_1)$  is shown in Fig. 3. The protection provided by an increasing number of ATs is clearly seen when the immunity parameter is not too small. For very small  $I$ , protection is only effective when the juvenile is completely surrounded by adults, i.e.  $S_1 = 8$ .

To better quantify the impact of the protection effect on juvenile survival and recruitment, we now estimate how the number of adult trees  $S_1$  in the near neighborhood of a site affects the recruitment probability  $P_R(S_1)$  defined as the probability that a grass site becomes successfully colonized by a tree seed during a given time-step and the resulting JT survives successive fires and becomes an adult. This probability is a product of several factors.

First, the grass site should receive in that time step a seed from the adult trees in the near or in the far neighborhood (the numbers of adult trees there are  $S_1 \in (0, 8)$  and  $S_2 \in (0, 16)$ , respectively). This is given by  $P_s(S_1, S_2) = 1 - (1 - b\Delta t/24)^{S_1+S_2}$ . Then, the seed establishes as a juvenile tree and must survive competition during successive time steps, which is given by the factor  $P_C^{Surv} = \exp(-\delta S_1)$ . Since  $m^{-1}$  is the average growth time from juvenile to adult tree,  $(m\Delta t)^{-1}$  time steps occur during growth,

and  $\exp(-\frac{\delta S_1}{m\Delta t})$  is the total survival factor to adulthood under competition.

Finally, the growing JT should resist the first and successive fires occurring during its growing time  $m^{-1}$ . The probability of surviving a single fire is the function  $P_F^{Surv}(S_1)$  numerically calculated and shown in Fig. 3 for the case in which the focal site is surrounded by  $S_1$  trees in the near neighborhood (i.e.,  $S_2 = 0$ ). An estimation of the probability surviving successive fires, which neglects any correlations arising from successive fire fronts and from the lattice configuration beyond the immediate neighborhoods, would be  $(P_F^{Surv}(S_1))^{f/m}$ , where  $f/m$  is the expected number of fires suffered by the JT during its growing time  $m^{-1}$ . The probability  $P_s(S_1, S_2)$  depends on the number of AT both in the near and in the far neighborhood. For consistency with the calculation of  $P_F^{Surv}(S_1)$  we will take  $S_2 = 0$ . This (as in the case of  $P_F^{Surv}(S_1)$ ) will underestimate the probability of establishment, survival and recruitment, as the trees in the far neighborhood do not compete with the central one. In this way we will obtain an estimation of the recruitment probability  $P_R(S_1)$  that is smaller than the exact one. Thus, if this function shows positive effects of surrounding adult trees, the exact result must be larger, since our approximation is obtained in a *worst case* situation.

Summarizing all the factors above, with  $S_2 = 0$ , our estimation of the recruitment probability of a grass site surrounded by  $S_1$  adult trees is

$$P_R(S_1) \approx \left[ 1 - \left( 1 - \frac{b\Delta t}{24} \right)^{S_1} \right] e^{-\frac{\delta S_1}{m\Delta t}} (P_F^{Surv}(S_1))^{\frac{f}{m}} \quad (1)$$

This is plotted in Fig. 4, and reveals both the positive and the negative effects of the presence of neighboring trees (but remember that the positive effects are underestimated). For medium values of the competition parameter

and above four neighboring adult trees the positive protective effect of fire (in combination with local dispersal) overcomes the negative effect of direct competition (see Figure 4(a) and (c)), but for high values of competition the negative effect predominates (see Figure 4(b)). For frequent fire, however, the protection effect is no longer effective.

## 6. Clustering patterns

### 6.1. Tree spatial pattern under different fire scenarios

We characterize spatial patterns of adult trees by the pair correlation function (Dieckmann et al., 2001),  $g(l)$ :

$$g(l) = \frac{\rho_{AA}(l)}{(\rho_A)^2} \quad (2)$$

where  $\rho_{AA}$  is the proportion of pairs of adult trees at a distance  $l$  (with respect to the total number of pairs of sites at that distance) and the denominator is the expected value of this proportion under a random distribution with the density of the adult trees  $\rho_A$ . At large distances  $g(l)$  is expected to approach 1, as correlations indicating a departure from random distribution would decay. For short distances,  $g(l)$  characterizes how the trees are packed together (see Dieckmann et al., 2001, chap. 14), values higher than 1 indicating a proportion of pairs at that distance greater than in the random case (clustering), and a smaller proportion indicated by values of  $g$  smaller than 1 (revealing a more regular spacing). We will not use the Euclidean distance for  $l$  but instead we will measure  $l$  in number of cell layers so that  $g(1)$  and  $g(2)$  will denote the pair correlation function for the first and for the second Moore neighborhood, respectively.

Comparison of Figure 5 with the results of Calabrese et al. (2010) shows that all the patterns found in the SM are also present here. Some features of the patterns can be understood from the fact that there is direct competition only between nearest neighbors, whereas the facilitation effect of local seed dispersal reaches first and second neighbors. In consequence, all these patterns have an enhanced probability of ATs having other ATs as second neighbors (far Moore neighborhood), as seen by the high value of  $g(2)$ . As in Calabrese et al. (2010), two types of configurations are distinguished by having a value of  $g(1)$  smaller or larger than 1, i.e. smaller or larger proportion of ATs in the near neighborhood than the one expected from a random distribution. The balance between positive and negative tree-tree interaction effects determines these values. The case  $g(1) < 1$  is a *regular* case in which trees appear more regularly spaced than in the random case. The case  $g(1) > 1$  is a *clumped state*, in which, although the density of near-neighbor pairs is still smaller than the one of far-neighbor pairs, it is larger than in the random case. The transition between the two states was governed by the parameter  $\sigma$  in the SM, which controls the probability of surviving fire. Here, this transition is determined by the explicit fire parameter  $f$ .

In the clumped patterns just described, further illustrated by Fig. 6(a) and (b), the clusters are *open* in the sense that there are more neighbors in the far neighborhood than in the near neighborhood. This is a clear effect of the competition existing in the near neighborhood, and was the only clumped state present in the previous SM. The novelty here is that, in addition, there is a second type of clustered state not present in the SM. A clumped state made of *closed* clusters is illustrated by figure 6(c) and (d). The clusters are

closed in the sense that there are more AT neighbors in the near neighborhood than in the far neighborhood. Thus, the positive effect of fire protection (and local dispersal) has completely overcome the competition effect occurring in the near neighborhood. The transition from one type of pattern to the other occurs when changing the competition or the lightning parameters,  $\delta$  and  $f$ , as shown in Figure 7.

### *6.2. Cluster-size distributions*

A cluster is a group of neighboring sites occupied by the same type of vegetation (e.g. adult trees). The distribution of cluster sizes is a powerful indicator of the different mechanisms occurring in ecosystems (Pascual et al., 2002; Pascual and Guichard, 2005). Adult tree cluster-size distributions in the Kalahari have been investigated by Scanlon et al. (2007), finding that in most cases a power-law fit can describe the data (although the fit was not of uniform quality). Scanlon et al. (2007) showed that resource constraints, together with positive local interactions of the type identified in the previous section, could generate cluster-size distributions similar to the observed ones.

Figure 8 shows complementary cumulative distributions of adult-tree cluster sizes from our model, where the Moore neighborhood has been used to



define clusters. Though the distributions have fat tails (see Fig. 8), a single power law does not provide a good description in the realistic range of parameters considered above. Also, the plateau at large sizes in the small- $f$  curves of Fig. 8 indicate the presence of clusters much larger than the rest. By artificially changing parameters to other ranges, one can find situations in which the cluster-size distribution follows a relatively good power law. This happens, for example, for  $\alpha = \beta = 1$ ,  $\delta = 0.01$ , and  $f \approx 0.9$ . Inspection of the tree distributions above and below this  $f$ -value indicates that a percolation transition occurs precisely at that point: there is a giant AT cluster spanning the whole area for smaller  $f$  values, and disconnected tree patches for higher values. Power-law cluster distributions are observed then close to this percolation transition, as in the mechanism discussed in Pascual and Guichard (2005), although in a narrower parameter range than suggested there. This transition is not attained within the parameter ranges considered before in this paper: tree cover in Fig. 8 is just of 0.4 for  $f \approx 0.9$ , and can not be increased much more (see Fig. 1, right panel), which makes it difficult to attain percolation through the whole lattice because of the absence of very large clusters. By artificially changing parameters to obtain larger tree densities, percolation becomes easier. In such situations, we observe more robust power-law behavior (not shown), but the system is then closer to a forest than to a realistic savanna. We do not find systematic correlation between the small-scale character of the tree patterns (regular, clumped, open, closed, ...) and the type of cluster-size distributions, despite the fact that one could expect that positive short-range correlations would favor power-laws (Scanlon et al., 2007).

## 7. Summary

We have introduced a model for savanna structure which includes, in addition to fundamental ecological interactions including competition, the effects of spatially explicit fire spread. Fire introduces some effective tree-grass and tree-tree interactions which are important in shaping tree demography and spatial pattern. First, the presence of fire improves competitiveness of grass because of its faster post-fire recovery. Second, adult trees may protect nearby juveniles from fire. This results in a positive tree-tree interaction which can, in some circumstances, overcome the effects of tree-tree competition for resources. A variety of tree spatial distributions are observed as a result of these direct and indirect interactions, which we have characterized by the pair correlation function and the cluster-size distribution. As the short-range positive interactions gain importance relative to the negative ones, a succession of regular to clumped states is observed. Clumped states can have “open” clusters, like the ones present in the previous SF model (Calabrese et al., 2010), but also “closed” clusters for the cases with stronger positive interactions. Adult-tree cluster-size distributions are of power-law type in some cases because of the proximity to a percolation transition, but for much of the realistic parameter range tree cover is small and far from percolating. The tails of the distributions, although fat, seem to decay faster than power laws, as seen in fact to occur in several of the sites reported by Scanlon et al. (2007).

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## Figures

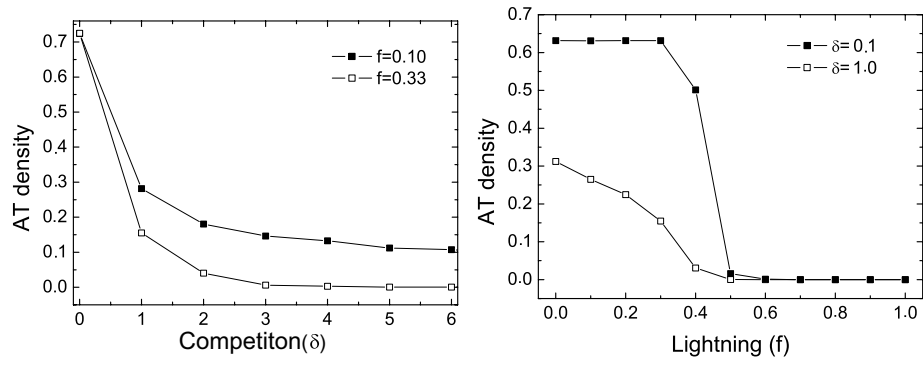


Figure 1: Density of adult trees (i.e., the number of adult trees divided by the total number of lattice sites) versus competition ( $\delta$ , left graph) and versus lightning ( $f$ , right graph). Average over 500 snapshots in the long-time asymptotic state. Parameters are as in Table 1. Transition from the coexistence state to grassland is driven by increasing  $\delta$  and/or  $f$ .

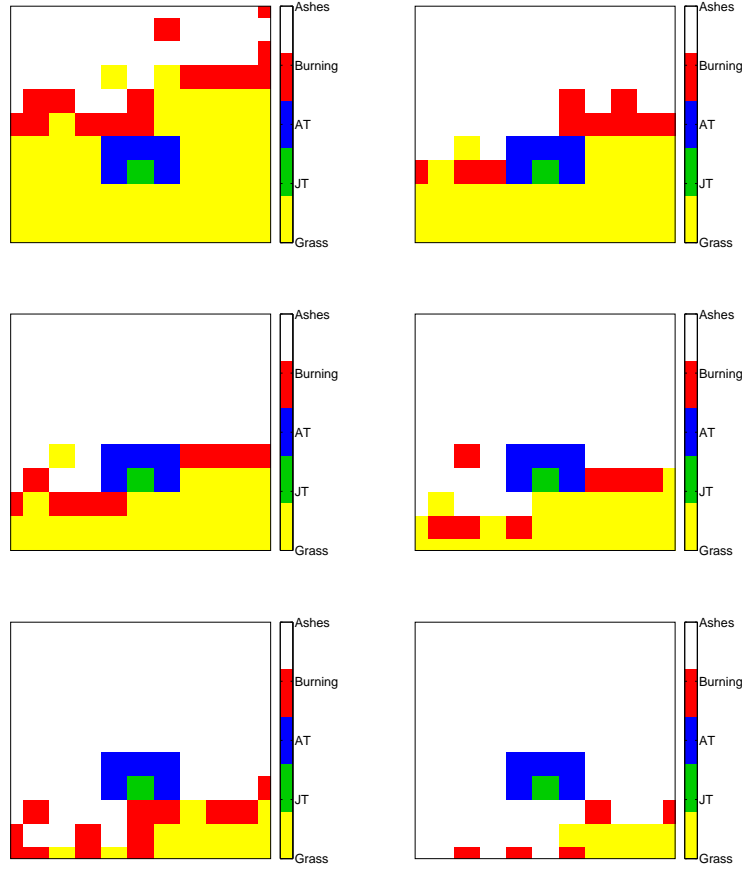


Figure 2: Protection effect: Selected snapshots from an example simulation with 5 adult trees (blue) surrounding a juvenile (green). Immunity parameter  $I = 0.3$ . Time runs from left to right and then from the upper to the lower row. A fire front (red) advances downwards, converting grass (yellow) into ashes (white), but the juvenile survives. Only a  $10 \times 10$  area of the whole  $200 \times 200$  lattice is shown.

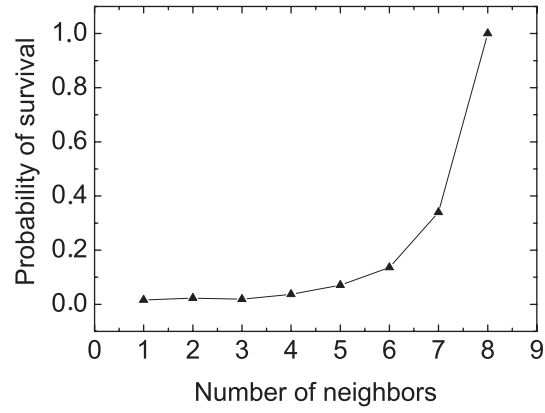


Figure 3: The protection effect: The probability  $P_F^{Surv}(S_1)$  of a juvenile surviving one fire as a function of the number of surrounding adult trees in its first neighborhood. This probability has been obtained from 1000 realizations of the process in which fire is initiated at one grass site, as described in the text, using immunity  $I = 0.3$ .

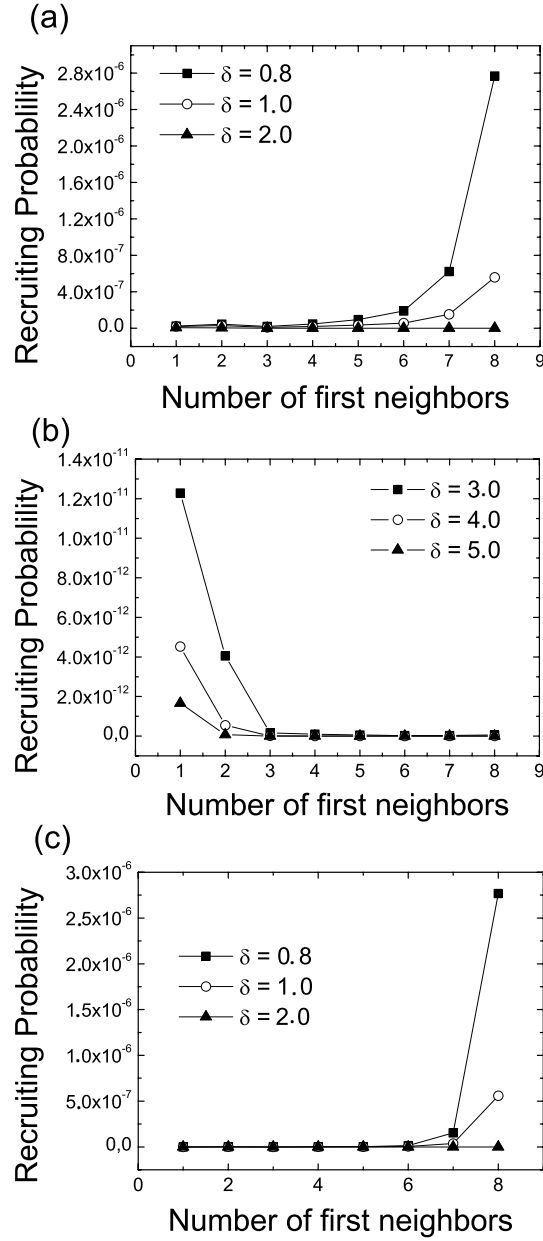


Figure 4: Estimation of the recruiting probability  $P_R(S_1)$ , as a function of the number of adult trees  $S_1$  in the near neighborhood, from Eq. (1), showing the positive and negative effects of these neighbors. (a) and (b)  $I = 0.3$ ,  $f = 0.33 \text{ year}^{-1}$  (triennial fire). (c)  $I = 0.3$ ,  $f = 0.2 \text{ year}^{-1}$  (pentannual fire).

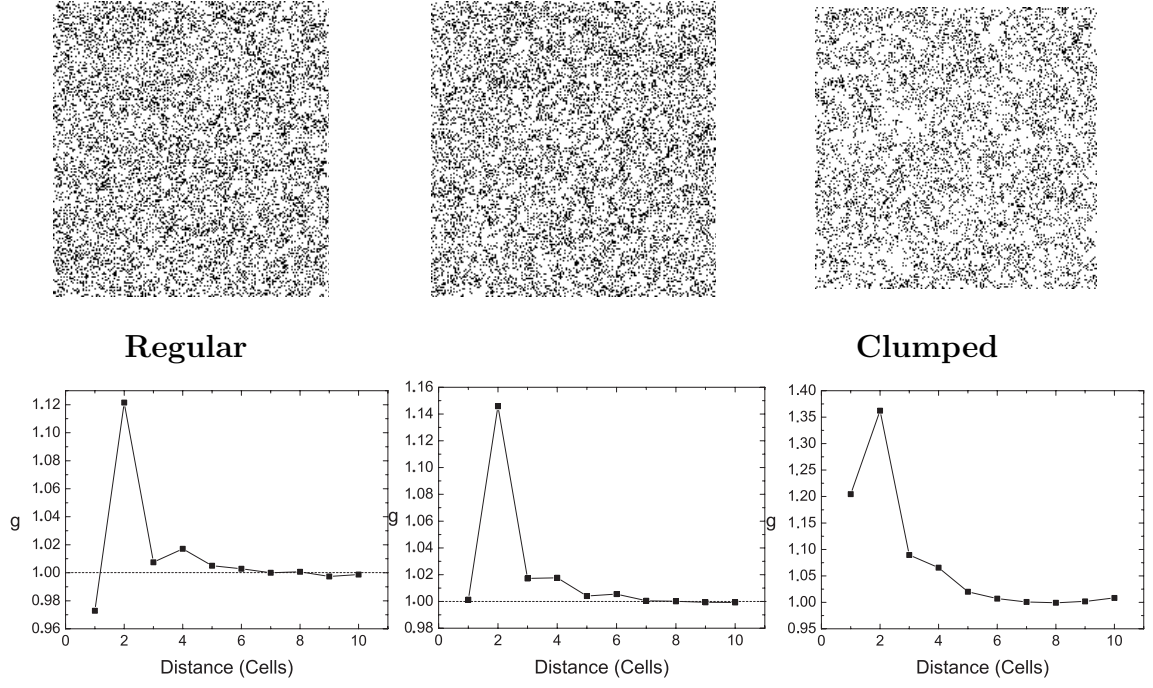


Figure 5: Patterns in the SFM. Parameters as in Table 1 and  $\delta = 0.01$ . Regular case:  $f = 0.19$ . Clumped case:  $f = 0.31$ . The central panel shows an intermediate state ( $f = 0.223$ ) in which  $g(1) = 1$ , which indicates the same number of AT near pairs as in a random case.

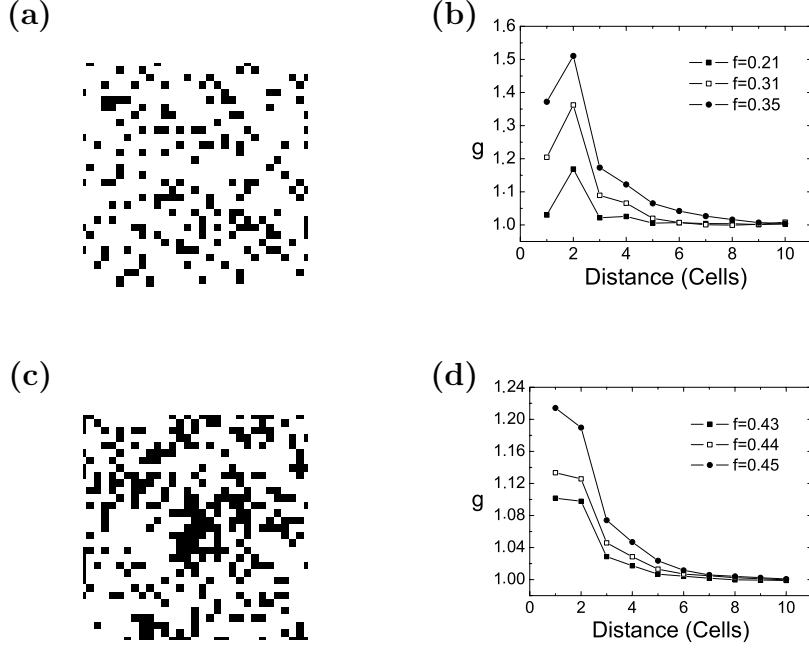


Figure 6: Savanna configuration in the clumped state at parameters as in Table 1. Panels (a) and (c) display only a  $30 \times 30$  portion of the full  $200 \times 200$  lattice. (a)  $\delta = 0.01$ ,  $f = 0.31$ : an example of open cluster of ATs, the typical configuration at these parameters. (b) Pair correlation function, similar to the one in the SM in the clumped state. (c)  $\delta = 0.001$ ,  $f = 0.45$ : an example of closed cluster of ATs, the typical configuration at these parameters. (d) Pair correlation function, which is different to the one in the SM in the clumped state because the maximum of  $g(l)$  occurs at  $l = 1$ , i.e. in the near neighborhood.

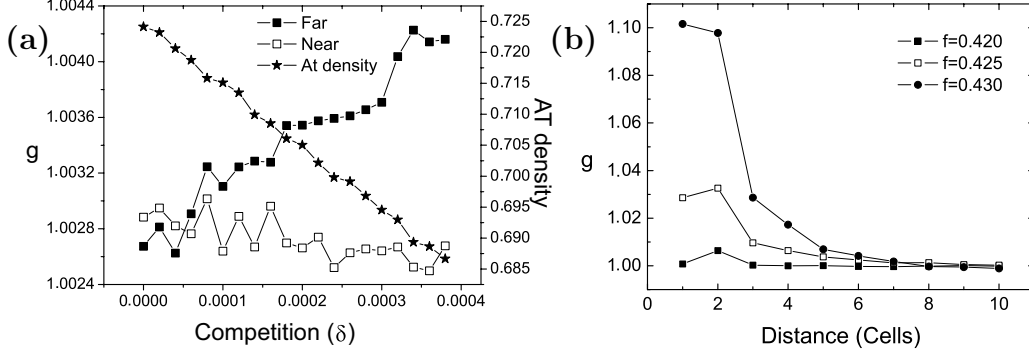


Figure 7: (a) Values of the pair correlation function for near neighbor pairs  $g(1)$  and for far neighbors  $g(2)$ , and values of adult-tree density, both as a function of the tree-competition coefficient  $\delta$ . Closed clusters occur for  $\delta < 5.2 \cdot 10^{-5}$  and open ones for  $\delta > 5.2 \cdot 10^{-5}$ . (b)  $\delta = 0.001$ , Pair correlation functions showing the transition between open ( $g(1) < g(2)$ ) and closed ( $g(1) > g(2)$ ) clusters by increasing  $f$ . Other parameters in both panels as in Table 1.

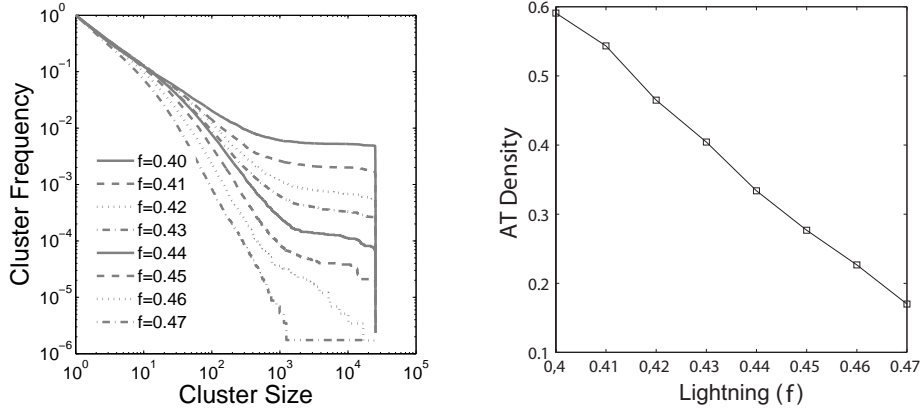


Figure 8: Left: Adult-tree cluster-size distributions, represented by means of the complementary cumulative distributions. Parameters as in Table 1 but  $\delta = 0.001$ . Right: Density of adult trees (i.e., the number of adult trees divided by the total number of lattice sites) versus lightning  $f$ .